E-Article

Shifts in Mass Scaling of Respiration, Feeding, and Growth Rates across Life-Form Transitions in Marine Pelagic Organisms

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abstract: The metabolic rate of organisms may be viewed as a basic property from which other vital rates and many ecological patterns emerge and that follows a universal allometric mass scaling law, or it may be considered a property of the organism that emerges as a result of the adaptation to the environment, with consequently fewer universal mass scaling properties. Here, we examine the mass scaling of respiration and maximum feeding (clearance and ingestion rates) and growth rates of heterotrophic pelagic organisms over an $\sim 10^{15}$ range in body mass. We show that clearance and respiration rates have life-form-dependent allometries that have similar scaling but different intercepts, such that the mass-specific rates converge on a rather narrow size-independent range. In contrast, ingestion and growth rates follow a near-universal taxa-independent ~3/4 mass scaling power law. We argue that the declining mass-specific clearance rates with size within taxa is related to the inherent decrease in feeding efficiency of any particular feeding mode. The transitions between feeding mode and simultaneous transitions in clearance and respiration rates may then represent adaptations to the food environment and be the result of the optimization of trade-offs that allow sufficient feeding and growth rates to balance mortality.

Keywords: metabolic scaling, body size, plankton, feeding modes.

Introduction

The vital rates of organisms depend on their size: feeding, metabolism, and growth rates all increase allometrically with organism size, typically such that the mass-specific rates decline with body mass (Peters 1983). This size dependency of energy flow and transformation ultimately determines the size structure of ecosystems (Andersen and Beyer 2006). This has probably been most explicitly described in the metabolic theory of ecology (MTE), which argues that the metabolic rate is the fundamental property of organisms that governs many other patterns in ecology, including growth and feeding rates, life histories, population growth, ecosystem structure, and productivity (Brown et al. 2004). The MTE rationalizes Kleiber's 3/4 power law for metabolic scaling from first principles, based on ideas of fractal branching distribution networks (e.g., West et al. 1997), and it argues that the law applies universally, from the smallest to the largest organisms (West and Brown 2005).

Empirically and/or theoretically supported scaling laws have similarly been proposed for other vital rates, such as feeding and growth rates, both within and across taxa (e.g., Fenchel 1986; Hansen et al. 1997; Ernest et al. 2003). Theoreticians still argue about the rationale of MTE, particularly the foundations for the metabolic scaling law (reviewed by Glazier 2010), and empiricists have not convincingly been able to decide on the magnitude and generality of the exponent of the power law or on the existence of one universal metabolic scaling law (Hemmingsen 1960; Banse 1982; DeLong et al. 2010). In fact, recent evidence suggests that mass-specific metabolic rates vary within a rather narrow range due to transitions in scaling properties between life forms (Makarieva et al. 2008).

Implicit in the MTE is that organism properties and life histories follow from metabolic constraints. However, organism biology, including life histories, and feeding and metabolic rates are not only determined by internal constraints governed by organism size but are also the result of adaptations to the environment in which the organism lives. One can argue that the metabolic rate of an organism may at least partly be an emergent rather than a fundamental property. This viewpoint is maintained by competing metabolic theories, for example, the dynamic energy budget (Kooijman 1986; Kearney and White 2012) and

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the metabolic-level boundaries hypotheses (Glazier 2010), which lead to predictions of different and variable metabolic scaling relations (exponents 2/3 to 1).

The most fundamental activities of any organism, namely, to eat, survive, grow, and reproduce, are interrelated through trade-offs and shaped by natural selection to optimize the fitness of the individual in the environment. The same environment is experienced differently by organisms of different sizes. For pelagic organisms, for example, fundamental properties of the environment depend on the size of the organism. Large organisms live in a world governed by inertia and where mass transport is by advection, while small organisms experience the same environment as viscous and transport of food and solutes is dominated by diffusion processes. The availability of food in the ocean is typically very low compared to terrestrial systems and generally decreases with size of pelagic organisms, and the method and metabolic cost of food collection consequently vary with size (Kiørboe 2011). Furthermore, the optimal allocation of matter and energy to growth, reproduction, maintenance, and defense (survival) may be very different for different life forms and feeding modes, for example, between gelatinous and nongelatinous plankton, between unicellular and metazoan zooplankton, or between ambush feeders and cruise feeders. This may lead to different allometries of vital rates between different life forms and organism sizes in the ocean. Similar arguments may apply to organisms living in other environments.

Eventually, the rate of food (energy) acquisition may constrain metabolic and other vital rates. Feeding rates of pelagic animals vary with food availability and the functional response can be characterized by two properties: (i) the maximum clearance rate, which is the imaginary volume of water cleared of prey items per unit time when the prey concentration is low; and (ii) the maximum ingestion rate, which is the feeding rate at a nonlimiting concentration of food. These two properties may scale differently with body size: the first is governed by the rate of transport of food to the organism, whether dominated by diffusive or advective processes (i.e., feeding current or locomotion of the predator); the latter is governed by the rate at which food can be handled and/or transported across surfaces. Pelagic organisms are often food limited (Huntley and Boyd 1984; Hirst and Bunker 2002; López-Urrutia et al. 2003), and the functional response may be adapted to optimize feeding rate in the real ocean. Other vital rates may similarly be adapted to environmental conditions with potential consequences for mass scaling properties (e.g., Witting 1995; Pawar et al. 2012). Examining a variety of rate processes in organisms within a single environment type is a clear way to test the degree of universality of scaling.

Here, we test the null hypothesis that different vital rates in pelagic organisms follow similar and universal mass scaling relations, both within and across taxa. We compile data from the literature in order to examine the mass scaling of feeding (maximum clearance and ingestion rates), respiration, and growth rates of pelagic organisms, from micron-sized heterotrophic flagellates to pelagic fish and jellyfish. We show that clearance and respiration rates have taxon- or life-form-dependent allometries and that the mass-specific rates converge on a rather narrow size-independent range, while maximum ingestion and growth rates are closer to taxon-independent Kleiber-type mass scaling.

Material and Methods

Data on body mass, maximum ingestion and clearance rates, respiration rates, and maximum growth rates of animals living in the ocean epipelagic were compiled from the literature, mainly from original articles, but also from previous compilations by other authors. Data were extracted from tables or digitized from graphs. Only measurements made on individuals of known size or groups of individuals of similar size were included. Further details on data selection and computation are given below for each of the vital rates. Body sizes were converted to carbon mass using standard conversion factors derived from a taxon-based synthesis (Kiørboe 2013) or other relevant conversions where necessary. We used taxon-specific conversions, thus ignoring differences between species, since these are minute relative to the range of body sizes examined. For example, for 10 pelagic taxa, the coefficient of variation of taxon-specific carbon content averages just 0.3 (Kiørboe 2013), while body masses in our compilation spans about 15 orders of magnitude. Rates were converted to a standard reference temperature of 15°C by assuming a Q_{10} of 2.8 (Hansen et al. 1997). This is roughly equivalent to assuming an "activation energy," E_a, of 0.65 eV for the typical temperature interval of the collected data (Acuña et al. 2011). While Q_{10} and E_a may both vary between taxa, taxa-specific information is insufficient, and we followed Hansen et al. (1997) and Acuña et al. (2011) in applying a common temperature correction. Altogether we collected 2,729 individual estimates of respiration rate, 871 estimates of maximum clearance rate, 327 estimates of maximum ingestion rates, and 852 estimates of maximum growth rates.

Ingestion and Clearance Rates

Ingestion and clearance rates depend on both the size and concentration of prey. We preferentially collected measurements taken at several prey concentrations and several

types (sizes) of prey, allowing prey-size specific estimates of maximum ingestion rate (i.e., ingestion rate at an unlimiting prey concentration, I_{max}) and maximum clearance rate (i.e., the clearance rate at a low prey concentration, F_{max}) from fits of functional response models to observations. In many cases, we digitized the data from the original articles and fitted an Ivlev model, but when possible we took the model reported. Two functional response models are preferentially used in the literature, Holling type II,

$$I = I_{max}\frac{F_{max}C}{I_{max} + F_{max}C}, \quad (1)$$

and Ivlev,

$$I = I_{max}\left[1 - \exp\left(\frac{-F_{max}C}{I_{max}}\right)\right], \quad (2)$$

where C is the prey concentration and I_{max} and F_{max} are the maximum ingestion and clearance rates, respectively. Fits of the two models yield similar parameter estimates, and hence, we did not attempt to refit to a consistently used model. In some cases, sigmoid functional response models had originally been fitted to the data; these were of somewhat variable mathematical form but still allowed estimation of the two parameters. This was done mathematically by estimating F_{max} as the first derivative of the ingestion formula at the concentration where the second derivative is 0 (i.e., $F_{max} = dI/dC$ at $d^2I/dC^2 = 0$). In some cases, fits of functional response models were not possible due to scarcity of data, but we could often still estimate the maximum clearance and ingestion rates as those reported for low and high prey concentrations, respectively.

Data allowing prey-size-specific estimates of I_{max} and F_{max} were in some cases possible for protozoans, copepods, euphausiids, and fish. For these, only data for optimal prey sizes were used in the comparative analysis, that is, the prey size that yielded the highest F_{max}. Data for euphausiids feeding on phytoplankton were avoided, unless feeding rates on several prey species were available and the highest rates could be selected, because feeding rates on zooplankton for most species is much higher. Tunicate data were rarely available for several prey concentrations or prey sizes, and hence, estimates of I_{max} and F_{max} for these groups are conservative. The same applies partly to fish and jellyfish. Here we used the data compilation of Acuña et al. (2011) as a starting point. For fish, we selected maximum clearance rates measured at low prey concentration and consulted the original articles to get maximum ingestion rates at high prey concentrations; for jellyfish, we did not attempt to estimate maximum ingestion rates since feeding rates in jellyfish often do not saturate in (short-term) laboratory experiments (e.g., Hanson and Kiørboe 2006). Data for protists were taken from Hansen et al. (1997) and supplemented with many new data from the primary literature. Data from all other groups were from original articles. All clearance and ingestion rate data are deposited in Pangaea, http://doi.pangaea.de/10.1594/PANGAEA.819856 (Kiørboe and Hirst 2013).

Respiration Rates

The respiration rate of an organism depends on its feeding and activity levels. For unicellular organisms, the respiration rate varies mainly with feeding level (e.g., Fenchel 1989), for larger organism more so with activity (e.g., Beamish 1978), and in both cases, the variation is within about 1 order of magnitude (except for "dormant" stages that in some taxa may reduce their metabolism to very low values). Ideally, one would like to compare "standard metabolic rates" (metabolism of nonfeeding organisms at rest), but in general it has been impossible to account for these factors in a standardized and meaningful way. This is because microbes are adapted to a feast-and-famine existence and may go into dormancy when starved. Furthermore, it is often impossible to control for activity in aquatic organisms (many have to move to stay afloat), and often organisms keep swimming or generating a feeding current even when starved. Thus, we have rather selected "routine rates" (rates recorded when organisms have normal activity) and have avoided measurements taken on dormant stages or individuals starved for prolonged periods of time. In all cases, metabolism has been quantified as rates of oxygen uptake. Data for fish and jellyfish respiration were taken from the compilation of Acuña et al. (2011) and the data for protozoans from Fenchel and Finlay (1983). Protozoans included "free-living" forms from both fresh and marine environments because it was impossible to decide on the habitat of many species. All other data were compiled from original articles. All respiration rate data are deposited in Pangaea, http://doi.pangaea.de/10.1594/PANGAEA.819850 (Kiørboe and Hirst 2013).

Growth Rates

Growth is a function of ingestion and food concentration, as well as of ontogeny. In order to standardize these rates, we considered only food-saturated growth rates of juvenile individuals. For protists, we added many new observations to the data compilation of Hansen et al. (1997). For metazoans, we began with the synthesis of Hirst et al. (2003), screening the compiled data for food saturated rates and adding data from new sources. For fish, we compiled data from the primary literature. Geometric mean masses were determined for the period in which growth in mass was measured, and all rates converted to mass-specific rates.

All growth rate data are deposited in Pangaea, http://doi.pangaea.de/10.1594/PANGAEA.819855 (Kiørboe and Hirst 2013).

Results

Respiration Rates

The respiration rates of all taxa increase with body mass and, when plotted together, scale approximately with body mass (fig. 1*A*). We also plotted mass-specific respiration rates since these plots better show differences in magnitude and scaling between taxa (fig. 1*B*–1*E*): the mass scaling of specific respiration rates within taxa are all consistent with a Kleiber-type scaling; that is, they are near proportional to body mass (carbon) raised to a power around $-1/4$ (table 1). However, the different taxa separate clearly, with subsequently larger taxa having increasing lead coefficients (intercepts), such that overall, specific respiration rates vary within ca. 2 orders of magnitude around a common value rather than declining with body mass. The protozoans have the lowest intercept, the two groups of copepods intermediate values, and other crustaceans (euphausiids and amphipods), tunicates, jellyfish, and fish, cluster around yet higher values. For comparison, we have shown also Kleiber's (1961) relation for terrestrial mammals that provide a conservative estimate for marine mammals (e.g., Lavigne et al. 1986); this relation fits into the general pattern and has the highest lead coefficient. The variation in the intercept of the mass specific respiration rates vary between protozoans and mammals by more than 3 orders of magnitude, inconsistent with a universal scaling law for metabolic rates (i.e., does not adhere to a single unified relation that fits both across and within taxa).

Clearance and Ingestion Rates

The variation in maximum clearance rates resembles that of respiration rates: the overall pattern suggests that clearance rates scale with body mass; within taxa, mass-specific clearance rates decline with body mass (fig. 2). Although these power terms are more variable than those for metabolic rates, for mass-specific rates they again vary around $-1/4$ (table 1). Over a 13-order-of-magnitude variation in body mass, average specific clearance rates vary by 3 orders of magnitude.

The mass-dependency of ingestion rates differs from those of respiration and clearance rates since the various taxa converge more closely on a common relationship, with ingestion rate increasing approximately with body mass to a power slightly larger than 3/4. Plots of mass-specific ingestion rates reveal a rather consistent decline across taxa, and the average of power exponents is not significantly different from $-1/4$ (fig. 3; table 1).

Growth Rates

Growth rates, like ingestion rates, converge on a common relation, with growth rate scaling with body mass to a power of about 3/4 or slightly higher. The specific rates show no consistent pattern between taxa and scale with mass with an average power of near $-1/4$ (fig. 4).

Discussion

A clear pattern emerges from the rather noisy data: respiration and clearance rates follow taxon-dependent mass scaling relations that are consistent with a 3/4 scaling law. However, when considered across taxa, scaling is close to 1. Consequently, the mass-specific respiration rates converge on a rather narrow, size-independent range, with the average rates varying within ~2 orders of magnitude over an 18-order-of-magnitude variation in body mass. A universal 3/4 or 2/3 scaling law would imply a variation in mass-specific rates by a factor 30,000 to 1,000,000, rather than the ca. 100-fold variation observed. Clearance rates follow a similar pattern, with no systematic size dependency when compared across taxa, albeit with larger variation between taxa. The Euphausiids (krill-like organisms) appear low; container effects that suppress feeding are known to occur in highly active Euphausiids, and ignoring those, the variation in mass specific clearance rates is again just 2 orders of magnitude. Ingestion and growth rates, in contrast, appear to follow more closely a universal 3/4 scaling law, with less consistent differences between taxa. These scaling patterns are apparent only when considered over a large range of body sizes. There may be significant deviations in mass scaling, both during ontogeny within a species and between species (e.g., Glazier 2005, 2006), but such variation is hidden in the current larger-scale analysis, which only emphasizes patterns that transcend the smaller-scale variations.

The lack of universality in the intercepts (elevation) of scaling relationships for organism metabolism is not a new observation, but it has been underappreciated for many years (Brown et al. 2004). Hemmingsen (1960) showed that unicellular eukaryotes and exothermic and endothermic organisms follow similar power laws but have nonoverlapping allometries, with endotherms having metabolic rates 2 orders of magnitude higher than unicellular organisms when corrected for body size. Banse (1982) also observed several transitions in metabolic scaling between groups of (mainly) pelagic organism. More recent reports have similarly demonstrated shifts in metabolic scaling between prokaryotes, protists, and metazoans (DeLong et al.

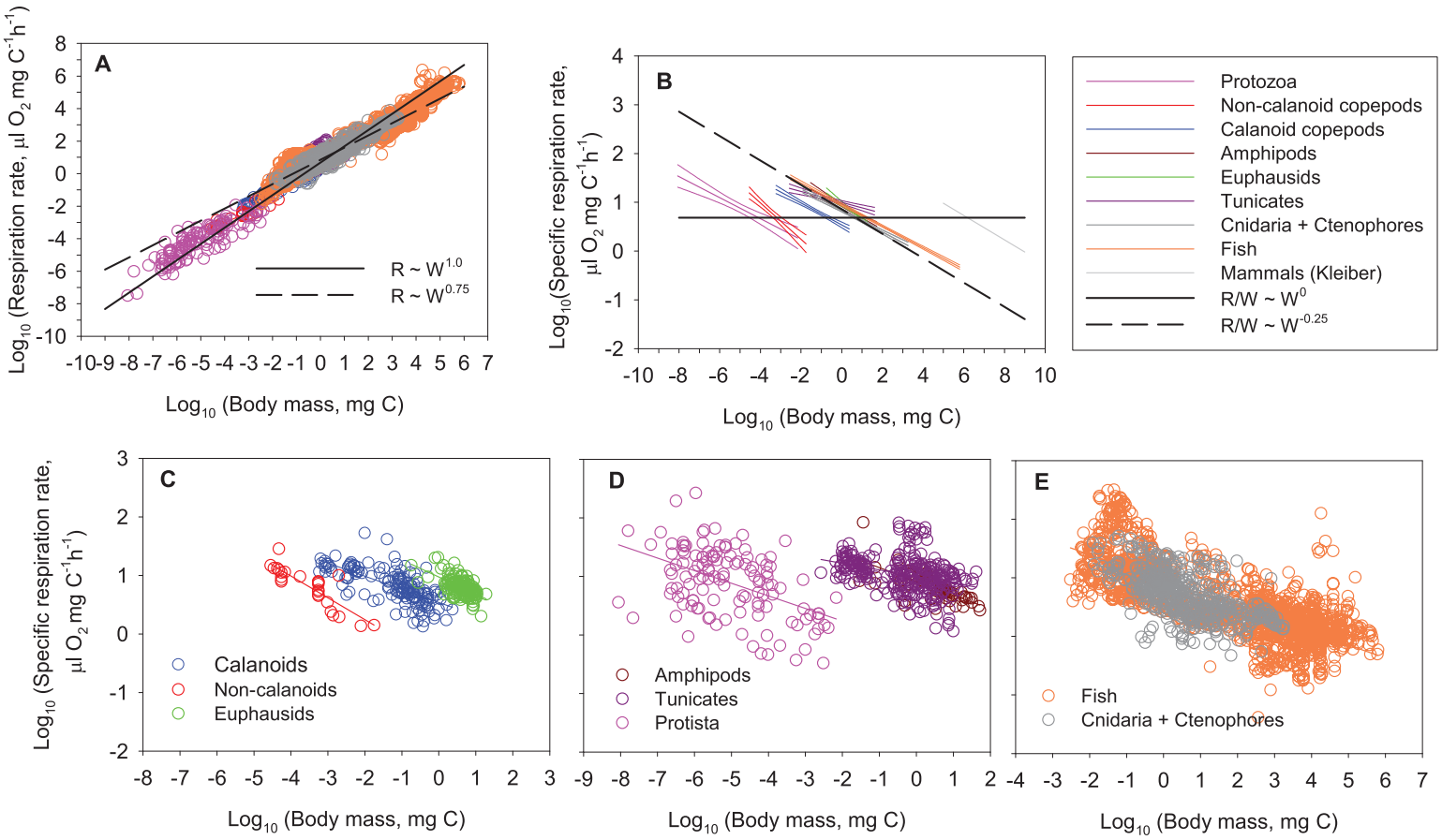

Figure 1: Respiration rates (*A*) or mass-specific respiration rates (*B–E*) of various groups of marine pelagic organisms as a function of their body carbon. All rates are converted to a common temperature of 15°C. *B*, Comparison of the regressions with 95% confidence limits for all taxa analyzed, including the line for mammals (Kleiber 1961); *C–E* show the same thing but include data points. *A*, *B*, Black lines show regressions through all data assuming proportionality between respiration rate and body mass or body mass raised to a power of 0.75 (*A*) or between mass-specific respiration rate and body mass raised to power 0 or −0.25 (*B*).

Table 1: Size dependency of mass-specific vital rates for pelagic animals

	Specific respiration rate (mL O_2 mg C^{-1} h^{-1})				Specific clearance rate (mL mg C^{-1} h^{-1})				Specific ingestion rate (μg C mg C^{-1} h^{-1})				Specific growth rate (mg C mg C^{-1} h^{-1})			
Group	Log *a*	*b*	R^2	*n*	Log *a*	*b*	R^2	*n*	Log *a*	*b*	R^2	*n*	Log *a*	*b*	R^2	*n*
Protozoa	−.20 ± .37	−.22 ± .07[a]	.23	129									−2.32 ± .30	−.15 ± .05[a]	.36	76
Flagellates	2.24 ± 2.26	.17 ± .34	.05	22	1.02 ± 1.21	−.23 ± .17[a]	.18	38	−.19 ± .80	−.33 ± .11[a]	.55	33	−3.23 ± .40	−.27 ± .06[a]	.69	41
Ciliates	−.49 ± .76	−.30 ± .15[a]	.30	76	−.52 ± 1.11	−.69 ± .2[a]	.66	25	1.29 ± 1.55	−.16 ± .28	.03	14	−1.69 ± .65	−.05 ± .12	.02	35
Calanoid copepods	.54 ± .06	−.22 ± .04[a]	.48	148	2.11 ± .31	−.16 ± .12[a]	.13	52	1.11 ± .17	−.20 ± .07[a]	.34	59	−2.17 ± .16	−.06 ± .06[a]	.03	136
Noncalanoid copepods	−.50 ± .34	−.37 ± .09[a]	.73	26	2.68 ± 1.57	.10 ± .43	.08	26	1.99 ± 1.05	.19 ± .29	.08	23	−3.47 ± 1.67	−.27 ± .41	.19	11
Other crustaceans													−2.82 ± .10	−.31 ± .09[a]	.25	139
Euphausids	.97 ± .05	−.29 ± .08[a]	.34	119	1.71 ± .29	−.37 ± .23[a]	.31	27	1.11 ± .56	−.14 ± .58	.04	10				
Amphipods	.92 ± .05	−.24 ± .06[a]	.50	61												
Chaetognaths					.96 ± .36	−.69 ± .37[a]	.93	4	−.06 ± .07	−.56 ± .07[a]	.77	79	−3.19 ± .49	−.35 ± .29[a]	.19	28
Cnidara + ctenophores	.83 ± .03	−.22 ± .02[a]	.38	568	2.68 ± .07	−.11 ± .05[a]	.04	364					−2.41 ± .08	−.15 ± .04[a]	.43	82
Cnidaria	.86 ± .03	−.21 ± .03[a]	.39	465	2.73 ± .07	−.12 ± .05[a]	.05	342					−2.41 ± .14	−.15 ± .10[a]	.27	31
Ctenophores	.76 ± .05	−.40 ± .06[a]	.60	100	2.09 ± .08	−.62 ± .09[a]	.91	20					−2.41 ± .10	−.15 ± .04[a]	.49	51
Tunicates	1.00 ± .04	−.11 ± .04[a]	.12	277	2.74 ± .08	.09 ± .04[a]	.06	261	1.91 ± .43	.28 ± .20[a]	.10	72	−3.23 ± .44	−.48 ± .19[a]	.37	46
Pisces	.96 ± .03	−.22 ± .01[a]	.59	1374	3.24 ± .21	−.24 ± .08[a]	.36	74	.40 ± 1.09	−.51 ± .32[a]	.19	45	−2.48 ± .04	−.17 ± .02[a]	.56	331
Average ± 95% CL		−.22 ± .13				−.30 ± .21				−.18 ± .25				−.23 ± .10		

Note: The averages ± 95% confidence limits (95% CL) in the bottom row are of the slopes of individual groups; only the lowest taxonomic units were included in the averaging (e.g., flagellates and ciliates, not protozoans). Regression parameters (±95% confidence limits) for mass-specific vital rate (respiration, clearance, ingestion, growth): log VR = log *a* + *b* log M, where VR is the mass-specific vital rate, M is the body mass (mg carbon), and *a* and *b* are the regression parameters. Term *n* is the number of observations, and R^2 is the coefficient of determination.

[a] Estimates of *b* that are significantly different from zero.

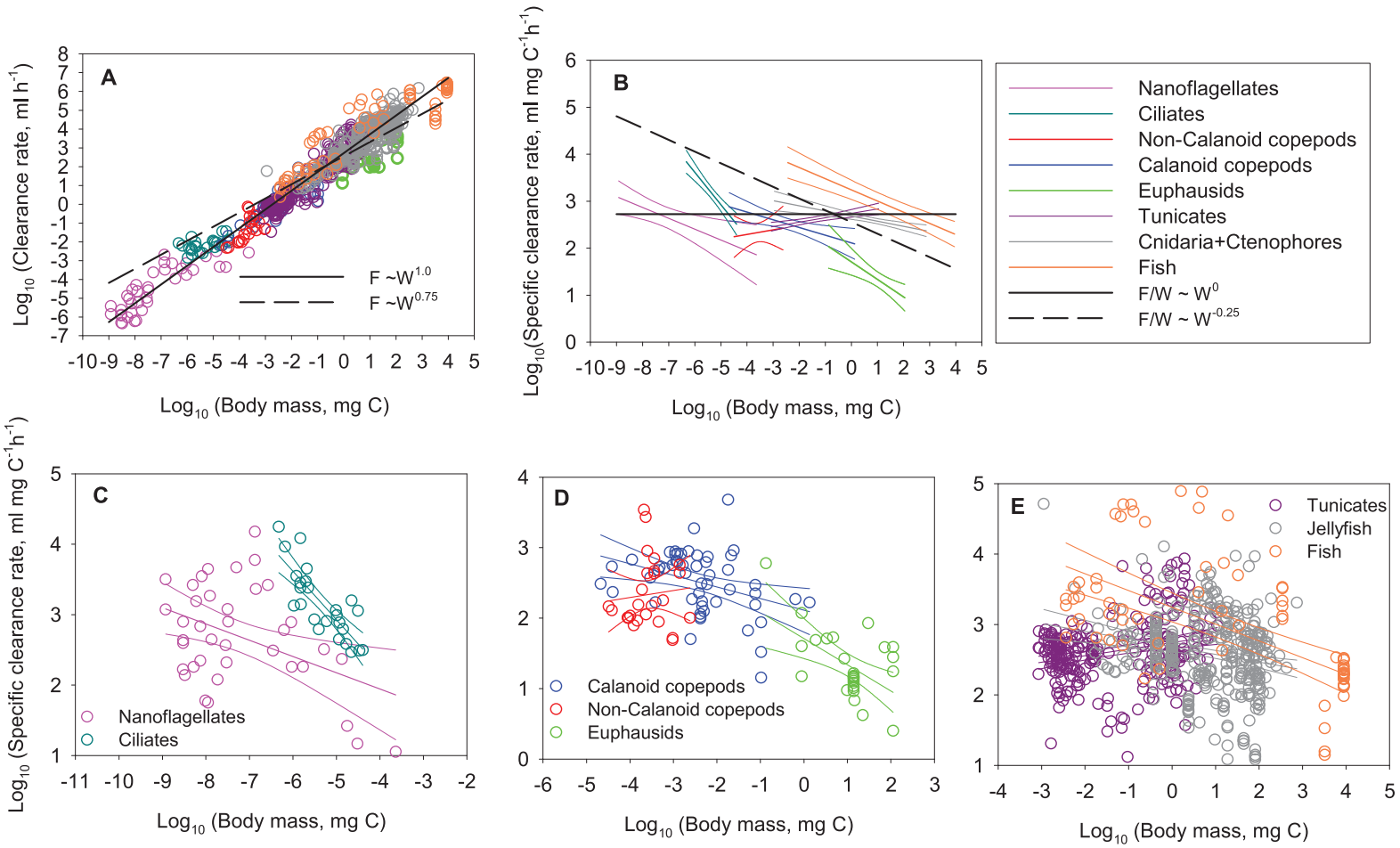

Figure 2: Maximum clearance rates (*A*) or mass-specific maximum clearance rates (*B–E*) of various groups of marine pelagic organisms as a function of their body carbon. All rates are converted to a common temperature of 15°C. *B*, Comparison of the regressions of specific rates with 95% confidence limits for all taxa analyzed; *C–E* show the same thing but include data points. *A*, *B*, Black lines show regressions through all data assuming proportionality between maximum clearance rate and body mass or body mass raised to a power of 0.75 (*A*) or between mass-specific maximum clearance rate and body mass raised to power 0 or −0.25 (*B*).

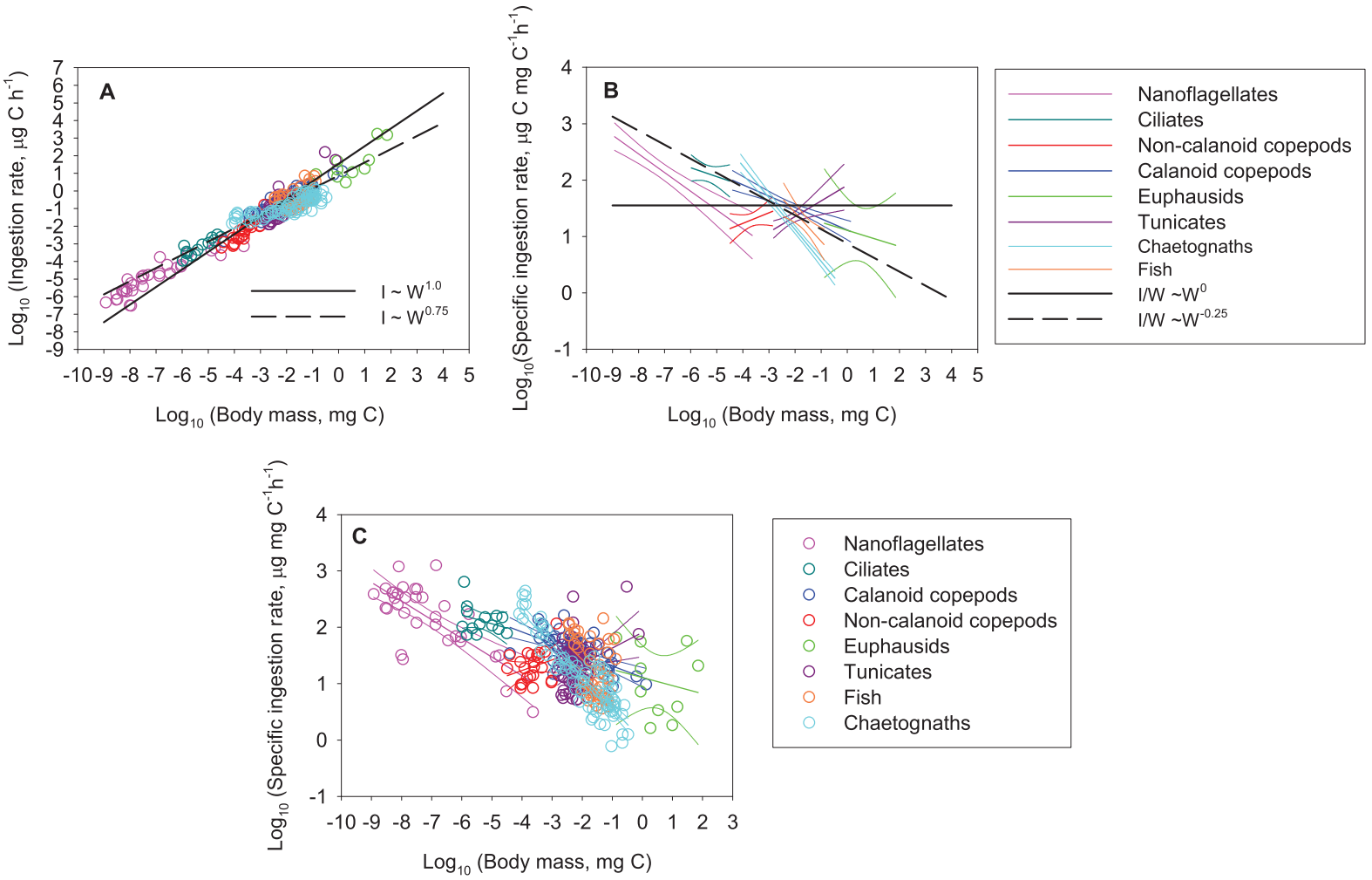

Figure 3: Maximum ingestion rates (*A*) or mass-specific maximum ingestion rates (*B*) of various groups of marine pelagic organisms as a function of their body carbon. All rates are converted to a common temperature of 15°C. *B*, Comparison of the regressions of specific rates with 95% confidence limits for the taxa analyzed; *C* shows the same thing but includes data points. *A*, *B*, Black lines show regressions through all data assuming proportionality between maximum ingestion rate and body mass or body mass raised to a power of 0.75 (*A*); or between mass-specific maximum ingestion rate and body mass raised to power 0 or −0.25 (*B*).

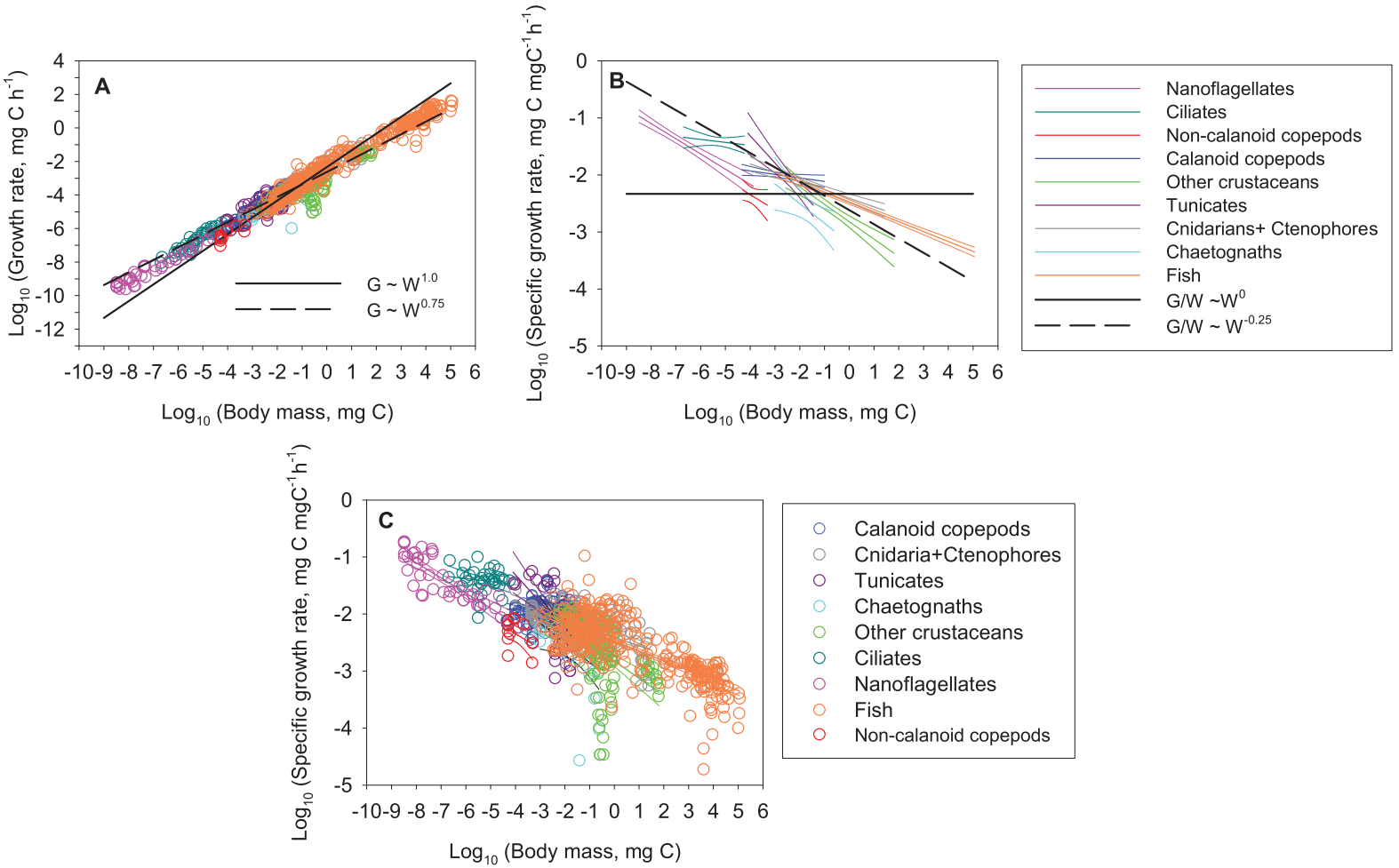

Figure 4: Maximum growth rates (*A*) or mass-specific maximum growth rates (*B*) of various groups of marine pelagic organisms as a function of their body carbon. All rates are converted to a common temperature of 15°C. *B*, Comparison of the regressions of specific rates with 95% confidence limits for the taxa analyzed; *C* shows the same thing but includes data points. *A*, *B*, Black lines show regressions through all data assuming proportionality between maximum growth rate and body mass or body mass raised to a power of 0.75 (*A*); or between mass-specific maximum growth rate and body mass raised to power 0 or −0.25 (*B*).

2010). Hemmingsen's groups correspond to the main ones in our material (fig. 1) and correspond, respectively, to the "invention" of multicellularity and homeothermy that may change the metabolic requirements of the organism. Our data, however, demonstrate additional and more continuous transitions among the metazoans organisms that may be related to life forms and feeding modes (see below), resulting in a striking similarity in mass-specific respiration rates across the entire range of organisms examined. A similar result was reported by Makarieva et al. (2008) based on an analysis of an extensive respiration data set covering a huge range of organism sizes, life forms, and habitats, from the smallest prokaryotes and plants to the largest mammals, and from aquatic to terrestrial environments. The redesigns that produce small shifts in respiration scaling powers but marked alteration in intercept are therefore not simply dependent on the macrodivisions of major evolutionary life-history events noted by Hemmingsen (1960) and DeLong et al. (2010). They are also attributable to rather more subtle redesigns related to life-form and possibly behavioral transitions. Makarieva et al (2008) argued for the existence of a "metabolic optimum," a universal metabolic rate magnitude that optimizes the fitness of organisms, but they did not rationalize its existence and magnitude.

Clearance rates show a mass scaling pattern that resembles that of the respiration rate, that is, with ~3/4 power relations within taxa but with size-independent specific clearance rates when all taxa and sizes are considered together. This is different from most previous reports, in which clearance rates of pelagic organisms were found to scale with mass to a power less than 1 (e.g., Fenchel 1986; Hansen et al. 1997; Saiz and Calbet 2007; Acuña et al. 2011). However, these articles all considered a much smaller range of organism sizes and taxa and hence may be dominated by within-taxa patterns. Is it possible to rationalize the taxa-transcending mass scaling of clearance rates? And is it possible to define and rationalize a "clearance optimum," similar to the metabolic optimum? That is, a clearance rate magnitude that optimizes the tradeoffs associated with feeding: energy gain versus cost in terms of energy and predation risks. The similarity in mass scaling of respiration and clearance may suggest a causal relationship, which is what we next want to turn to in this article.

One may argue that the clearance or search rate of an organism represents its own effort to acquire food. This effort implies energy demanding work as well as energy to produce and maintain food collection apparatus and sensory system. Maintenance and food collection may both potentially make a significant contribution to the metabolic rate of an organism and can apply even when that effort does not lead to resource acquisition; the machinery has to be maintained, and the organism may keep processing water in search for food even in its absence. There are a limited number of basic mechanisms used by pelagic organisms to concentrate food from a dilute environment. The efficiencies of these mechanisms, in terms of volumes cleared for prey, are inherently different, and each becomes less efficient with increasing body size (Kiørboe 2011), potentially explaining the consistent within-taxa decline in mass-specific clearance rates. Larger taxa must switch to more efficient and, presumably, more energy-demanding feeding modes and prey-sensing mechanisms to compensate for this general decline in efficiency. Food collection mechanisms in small aquatic organisms are dominated by "cheap" passive, diffusion-type processes that do not require perception of individual prey. As size increases, taxa use more efficient but expensive active "advective" processes, such as cruising or generating a feeding current, as well as costly remote prey-sensing mechanisms (chemical, hydromechanical, and visual). Thus, some small flagellates feeding on bacteria may depend mainly on the motility of the bacteria for prey encounter (Langlois et al. 2009). Flagellates with a feeding current may increase prey encounter rate, and swimming may enhance food acquisition by bringing the flagellate to food patches, but generating a feeding current and swimming at low Reynolds numbers is considered energetically inexpensive (Berg 1993; Guasto et al. 2012). The larger ciliates use multiple cilia to generate a more efficient feeding current (Magar and Pedley 2005; Short et al. 2006), which is presumably also more energetically expensive. Moving to the multicellular organisms, the small, noncalanoid copepods are mainly ambush feeders; that is, they hang motionless in the water waiting for prey to pass within their perceptive sphere (Kiørboe et al. 2010). The larger calanoid copepods and euphausiids produce more efficient and energetically expensive feeding currents (Kiørboe and Jiang 2013). In contrast to the unicellular flagellates and ciliates, the crustaceans (copepods and euphausiids) typically perceive individual prey using chemo- or mechanosensors (e.g., Abrahamsen et al. 2010; Tiselius et al. 2013), which requires maintenance of relatively advanced and energetically costly sensory systems (Niven and Laughlin 2008). As we move further up in size, the "inflated" (high water content) gelatinous plankton have increased capture surface areas per unit of organic matter, which allow for high clearance rates (Acuna 2001; Acuña et al. 2011), but this is also costly to maintain (Kiørboe 2013). The use of vision by fish results in more efficient remote perception of prey and consequently high clearance rates (Kiørboe 2011). While it is not possible to exactly quantify the metabolic expenses associated with the different feeding modes, we know that "active" is more expensive than "passive" and that the processing of sensory information, particularly vision, is metabolically expensive

(Laughlin et al. 1998). It is striking that the transitions in feeding modes largely follow the transitions in clearance and respiration scaling (figs. 1, 2). In fact, the lead coefficients of taxon-specific allometric fits of mass-dependent respiration and clearance are significantly and linearly related (fig. 5).

The trade-offs associated with food collection are not limited to the energetic gains and costs of feeding, but there are also associated predation risks (Visser 2007). Any definition of a clearance optimum should consider all trade-offs together. Kiørboe and Jiang (2013) evaluated these for intermediate-sized zooplankters and found that optimal foraging considerations predict an optimum magnitude and mass scaling of clearance rates consistent with that observed here, but their analysis was restricted to a limited size range (~6 orders of magnitude) and did not consider size-dependent variation in the availability of food. The average availability of food in the ocean tends to decline with increasing size of the predator (Kiørboe 2011), and hence, a constant feeding effort (mass-specific clearance rate) implies a decreasing mass-specific ingestion rate with size, as observed. This may be sufficient to maintain a population in the face of mortality, because mortality rates are also declining with organism size in the ocean (Peterson and Wroblewski 1984; McGurk 1986). In fact, specific ingestion rates and growth rates (figs. 3, 4), as well as intrinsic population growth (Fenchel 1973; Savage et al. 2004) and mortality rates (Peterson and Wroblewsky 1984; McGurk 1986) all appear to decline with body mass in a similar manner. Thus, observed differences and similarities in the mass scaling of different vital rates of pelagic organisms appear to be internally consistent. We hypothesize that the clearance rate magnitude and consequent feeding and growth rate is that required to balance mortality in the ocean and in that sense defines a clearance and metabolic rate optimum that maximizes the fitness of the organisms. Whatever the causal relation between feeding and metabolism in pelagic organisms, the lack of universal scaling relations has important implications for our understanding and descriptions of pelagic ecosystems.

Our observations and arguments have focused on pelagic organisms, but the mass scaling of respiration rate found here for pelagic organisms appears to mirror that found also for terrestrial organisms (Makarieva et al. 2008). Similar arguments as those applied here may be generalized to cover other environments and transitions

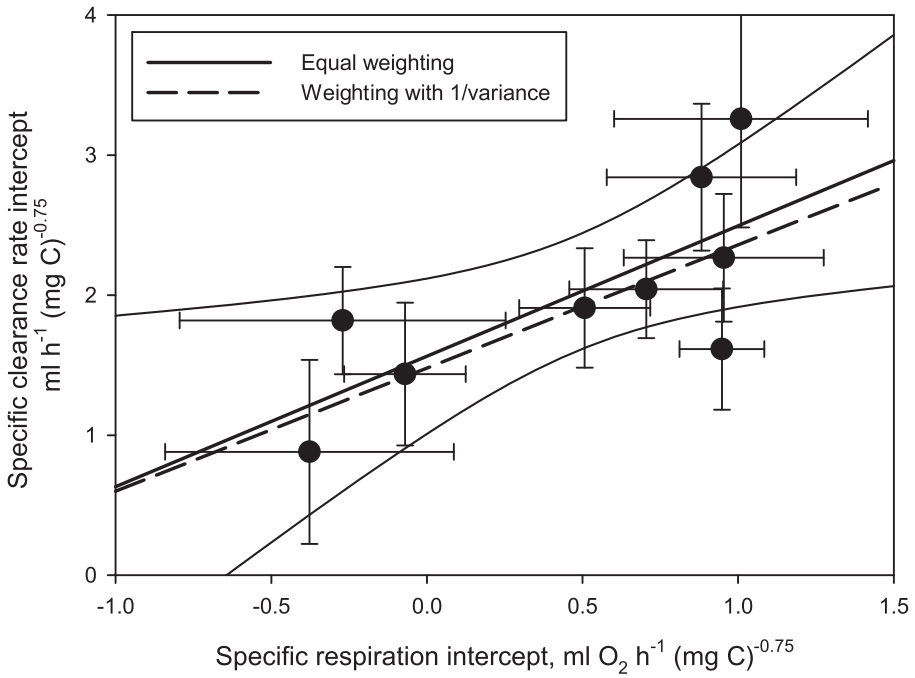

Figure 5: Intercepts values ($a \pm$ SD) for allometric regressions of mass-specific clearance rates and mass-specific respiration rates plotted against one another. The allometric regressions assume a Kleiber-type mass scaling (i.e., mass-specific respiration or clearance scale with mass raised to power of -0.25) and are of the form $\log_{10}(\mathrm{VR}) = a - 0.25 \log_{10} M$, where VR is the mass-specific respiration or clearance rate, and M the body mass (carbon). The regression lines are estimated with equal weight to all observations, or observations weighted with the inverse of variance of the a estimate. The regressions are $Y = 0.93X + 1.56$ (equal weight; $R^2 = 0.53$) and $Y = 0.88X + 1.48$. The correlations are in both cases statistically significant with $P < .02$.

in life forms. For example, adaptations to habitat dimensionality and transitions from sedentary life to surface motility to flying life styles are all related to both feeding modes and metabolic expenses (e.g., Pawar et al. 2012) and may show similar covariation in scaling of metabolism and clearance rates. The organisms included in our synthesis have trophic encounters that predominantly occur in three dimensions. Pawar et al.'s (2012) mechanistic model of three dimensions encounters suggests that both consumption rates and search rates (akin to clearance rate) should scale with body mass with a power ~1 but at less than 1 when encounters are in two dimensions, for example, for many terrestrial and benthic encounters. There are three important points that challenge Pawar et al.'s (2012) predictions. First, as we observed, maximum clearance rates (search rates) of individual taxa often scale at less than 1 (fig. 2; table 1), and our observations matches Pawar et al.'s conclusion only when considered across life forms, as in their own data compilation. Secondly, ingestion rates scale with mass both within and across taxa at less than 1 (fig. 3; table 1). Further support of subisometric scaling is found within taxa when reassessing Pawar et al.'s consumption data for copepods, insects, and fish. Together these include the vast majority of their empirical data set, and each of these taxa show scaling of less than 1. The next generation of mechanistic models needs to be developed so as to explain the differences in scaling of feeding and physiological rates that occur at different levels of organization. Indeed, multiple mechanisms may need to be evoked across organizational hierarchies. In pelagic invertebrates, for example, respiration commonly scales near isometrically intraspecifically (Glazier 2005, 2006) but close to 3/4 when considered within individual taxa and more steeply again when considered across multiple taxa (fig. 1; table 1; Makarieva et al. 2008). Many models, including that of Pawar et al. (2012) and the metabolic theory of ecology (Brown et al. 2004), do not make distinctions at these hierarchies and hence fail to match the patterns observed in nature.

The declining efficiency of each feeding mode with size implies that there is a maximum size above which it becomes impossible for that feeding mode to maintain a sufficient feeding rate. And there must also be a maximum size range for particular life forms or feeding modes. If we consider the 2-order-of-magnitude variation in specific metabolism and clearance the optimum range and a 3/4 mass scaling, then the maximum possible body mass variation within a particular life form is 8 orders of magnitude. This, in fact, corresponds roughly to the size range of each of the following: protozoans, pelagic crustaceans, gelatinous plankton, fish, and mammals.

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